Amer. Malac. Bull. **32**(2): 308–322 (2014) http://www.bioone.org/toc/malb/32/2

A new critical estimate of named species-level diversity of the recent Mollusca*

Gary Rosenberg

Department of Malacology, Academy of Natural Sciences, Drexel University, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103 U.S.A.

Correspondence, Gary Rosenberg: rosenberg.ansp@drexel.edu

Abstract: Modern estimates of species-level diversity in the recent Mollusca range from 34,000 to 120,000 described species, with total diversity including undescribed species often cited as 200,000. Most estimates are unverifiable, not being based on reproducible methods. Ultimately the best way to gauge diversity is explicit enumeration: actual listing of known species. Comprehensive lists of species are valued as a basis for systematic revisions and for comparing diversity across taxa, but it is less appreciated that they also provide a means for statistical sampling of biodiversity databases. I assessed the completeness of molluscan species listings in the World Register of Marine Species (WoRMS) by comparing it to a standardized inventory of the species represented in the Malacology collection of the Academy of Natural Sciences of Philadelphia (ANSP). Random samples of names were scored for presence or absence in WoRMS, with standard errors calculated from the binomial distribution. The WoRMS database has about 1,200 duplicate or extraneous listings for mollusk species and is missing about 1,300 (3%). Overall marine molluscan diversity is estimated at 43,600 ± 900 species, where 900 is a 95% confidence interval. The validity of this confidence interval depends on the WoRMS database and the ANSP collection not having correlated weaknesses. Lack of relatively complete species databases prevents similar assessments for terrestrial and freshwater mollusks, but, using less rigorous methods, I estimate that there are 70,000 to 76,000 described species of recent Mollusca.

The low end of this estimate, 70,000 species, is similar to the number of recent chordate species, 69,000, so it is possible that the Mollusca are not the second most diverse phylum of animals in terms of recognized recent species. Naming rates for chordate are currently higher than for mollusk, 750 versus 600 species per year, although the Mollusca are regarded as having higher undescribed diversity. The Mollusca have long been considered the most species-rich marine phylum, but the estimate of 43,600 is substantially below the 56,000 species of Arthropoda listed in WoRMS. Globally, the ratio of marine gastropod to marine bivalve species in WoRMS is 4:1, which is higher than in any regional fauna, suggesting that gastropods have smaller geographic ranges on average than bivalves. The main remaining gaps in WoRMS are among opisthobranchs (8% missing) and Indo-Pacific marine mollusks (6%). The most diverse molluscan genus in WoRMS is *Turbonilla*, with more than 1,000 species listed as accepted.

Key words: biodiversity, gastropod, bivalve, databases, random sampling

There have been many prior estimates of species-level diversity of recent mollusks, as summarized by Boss (1971) and Chapman (2011). Modern estimates of the number of named species range from 34,000 (Boss 1971) to 120,000 (Ponder *et al.* 2002) and of total diversity, including undescribed species, from 47,000 (Boss 1971) to the often cited 200,000 (Wells 1995, Groombridge and Jenkins 2002, Chapman 2011). My own estimates for described species have been 72,000 (sum of diversity by classes in Rosenberg 1992, p. 11–12) and 85,000 (cited by Chapman 2011, p. 34, as pers. comm.).

Most estimates do not state the methods used and are not verifiable, being essentially expert opinions, or summaries thereof. For example, Mayr (1969) listed molluscan diversity as 107,250 species without stating the source of his estimate. At the same time he listed avian diversity as 8,600 species, stating (p. 12): "In birds 99 percent of all living species have surely been described". Yet the number of bird species now recognized exceeds 10,500 (International Ornithologists' Union <http://www.worldbirdnames.org/>), an increase of 22%. Some of this gain, however, represents the elevation of subspecies and synonyms to full species rather than discovery of new species.

The uncertainty in estimating diversity in a well-known taxon such as Aves illustrates the need for considerable caution in estimating molluscan diversity. Figure 1 shows that

---

* From the "Mollusks: Magnitude of molluscan diversity – the known and the unknown" Symposium held at the 78th meeting of the American Malacological Society, Cherry Hill, New Jersey, June 19–20, 2012. Symposium manuscripts were reviewed and accepted by the Symposium Organizer and Guest Editor, Dr. Ira Richling.

the species discovery curve for marine mollusks has no sign of an asymptote. It is dangerous to extrapolate from such a curve, because it can change trajectory without any more species being described. Currently recognized taxa might be synonymized, and synonyms might be recognized as representing valid taxa. These changes would not be graphed in the year the classification changed, but in the year the taxon was named. Figure 1 does not show the number of species that were recognized in 1950 (for example); it shows the number of species currently recognized that had been named by 1950 (leaving aside the problem of renamed homonyms). Since extrapolating an asymptote in this situation is untenable, Figure 1 is best interpreted as showing that fewer than half of the species of marine mollusks have yet been discovered, since a point of inflection has not been reached on the curve.

Rather than trying to estimate the number of mollusk species that might ultimately be discovered, I focus here on determining how many have already been described. The best method for doing this is explicit enumeration, as advocated by Sykes (1901), that is, actual listing of known species. In general, estimates of molluscan diversity on the lower end take this approach, counting named species across taxa and faunas (Boss 1971). Figure 1 shows the results of explicit enumeration of species in the World Register of Marine Species (WoRMS, http://www.marinespecies.org/).

Since 2008, WoRMS has emerged as a global standard for marine molluscan taxonomy. Its main molluscan editors initially were Philippe Bouchet, Serge Gofas and me, with Bruce Marshall and Rüdiger Bieler joining in 2013 and 2014 respectively. More than 30 other editors have contributed to various families and superfamilies of Mollusca. Records created or last edited by taxonomic editors appear online as "verified" (with a green check mark) and records added or last edited by data management personnel (perhaps imported from another database or from uncritical checklists) appear as "unverified" (with a red question mark). The online database shows the editing history of each record, with the name of the person responsible for each change and a date-time stamp.

Comprehensive lists such as WoRMS are valued for providing the nomenclatural basis for systematic revisions and for comparing diversity across taxa, but it has been less appreciated that they also provide a means for statistical sampling of biodiversity databases. Although WoRMS is approaching completeness for valid species, it is less complete for synonyms. Also, it has some duplicate listings, and some that are out of scope (freshwater, terrestrial or fossil, but not flagged as such). I present methods here for understanding the scale of these problems in a statistical framework, along with methods for estimating how many named marine taxa are missing, and for estimating the diversity of terrestrial mollusk species in the absence of a global list of species.

The computerized inventory of the mollusk collection at ANSP has been a useful tool in this process. Since the beginning of 2011, the current placement in the collection of about 320,000 lots has been recorded in the department's collection database, including almost all of the gastropods. The inventory standardizes names across the database (for spellings and generic placements), allowing random sampling based on name. A taxonomic dictionary that links to the genus field gives the higher classification for each name. This dictionary also gives the habitat for each genus: as one or more of "marine", "brackish", "freshwater" and "terrestrial", which allows random sampling by those descriptors. For gastropods, the ANSP inventory is largely independent of the WoRMS database, as most work was completed before the WoRMS database was regarded as complete enough to guide curation, however, there are some areas of overlap. Triphoridae in WoRMS was compiled with reference to the ANSP collection and Patellogastropods at ANSP were curated against WoRMS.

The results for species diversity are similar to those I presented at the symposium in 2012, but have been entirely recalculated since October 2013 when I

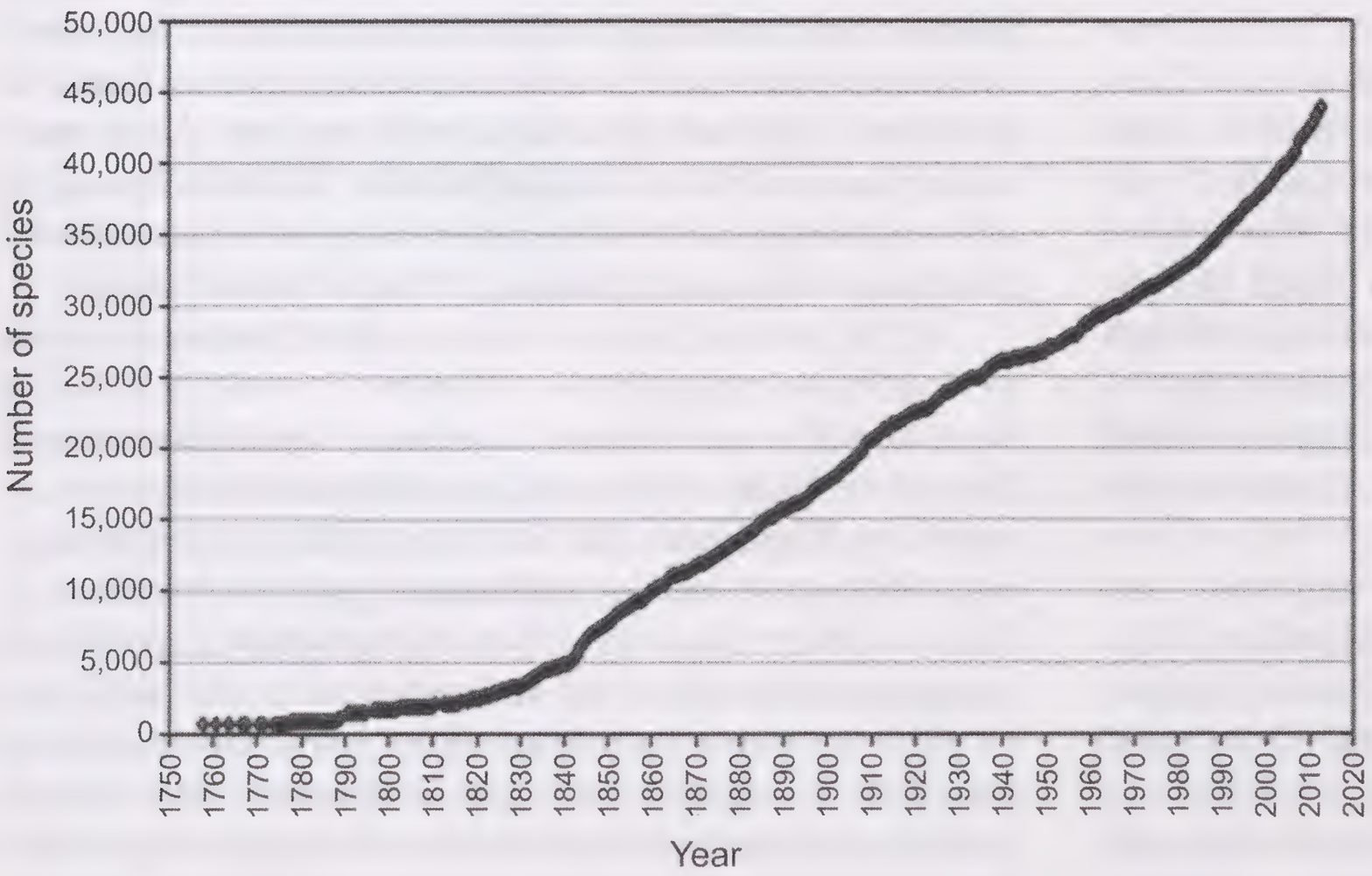

Figure 1. Species discovery curve showing species currently treated as valid in WoRMS cumulatively by year of description.

completed a major push to add data to WoRMS, focusing particularly on the Pyramidellidae, which had been underrepresented. Most of the molluscan classes had relatively little growth in that period (0–1.4%), but the Gastropoda grew by more than 10%, not including species named since June 2012. I had estimated then that WoRMS might be missing as much as 16% of gastropods, so closing that gap has been important for producing a more reliable estimate of marine molluscan diversity.

MATERIALS AND METHODS

To estimate error levels in WoRMS, I took "verified" and "unverified" names (see Introduction) of accepted species of Bivalvia and Gastropoda at random and queried based on the specific epithet to determine how many were duplicates, synonyms, or out of scope (*e.g.*, fossil only, freshwater only). "Duplicates" were defined as the same epithet applied to the same taxon being listed as "accepted" more than once under different generic combinations or different spellings. For example, both *Monodonta nigerrima* and *Diloma nigerrima* being listed as valid would be a duplicate, because both are based on *Turbo nigerrimus* Gmelin, 1791. *Tegula nigerrima* is not a duplicate of those names, however, as it is based on *Trochus nigerrimus* Gmelin, 1791, a different taxon. Similarly, unresolved homonyms would not be counted as duplicates: *Calliostoma canaliculatum* (Lightfoot, 1786) and *C. canaliculatum* (Sasao and Habe, 1973) are both accepted names in WoRMS because no replacement name is available for the junior secondary homonym.

Each epithet was used in truncated form in a "contains" search in the WoRMS "Scientific Name" field, "pulch", for example, matching *pulcher*, *pulchra*, *pulchrum*, *pulchellus*, *pulchella*, *pulchellum*, etc. The rank of the higher taxon in which the search was to be run (family, superfamily, order, etc.) was judged by the taxon. An epithet in Turridae, for example, would be searched in Conoidea, whereas one in Pyramidellidae would be searched in Gastropoda, as it might also be listed in Aclidae or even Rissoinidae.

Randomization was implemented by importing into Microsoft Excel 2010 all records from WoRMS with the target status (*e.g.*, verified, accepted species of bivalve) and assigning each record a random number using the "rand()" function. The records were then sorted lowest to highest by that number, and the first n records were evaluated, with $n = 50$ for verified accepted bivalves, $n = 100$ for unverified accepted gastropods and verified accepted bivalves and $n = 200$ for verified accepted gastropods.

Percentages of erroneous records were calculated as (duplicates/2 + synonyms + out of scope)/n. Duplicates were halved because a duplicate record is twice as likely as an unduplicated record to be selected at random. (In a database with 50% single records and 50% duplicate records, 25% of the records must be deleted to get rid of the duplicates.) The effect of triplicate records was assumed to be negligible, allowing calculation of standard errors based on the binomial distribution. For chi square tests, two-tailed p values were determined using the GraphPad online calculator, with degrees of freedom one less than the number of categories (http://graphpad.com/quickcalcs/chisquared1.cfm).

To find species missing from WoRMS, I sampled marine gastropod species at random from the ANSP mollusk collection inventory (see Introduction), as follows. For each species, the number of lots in the collection was determined, and a random number assigned. The spreadsheet was then sorted, first by number of lots, then by random number, and the first 200 names in each of five groups were selected starting at 1 lot, 5 lots, 10 lots, 20 lots and 40 lots, representing a gradient of "rare" to "common". The latter two groups spanned ranges of 20–22 and 40–51 lots, because ANSP did not have 200 marine gastropod species with the starting number of lots. The resulting 1000 names were matched against the WoRMS database using the genus and species epithets and the WoRMS automated matching tool. Names that matched exactly were accepted as matching without further investigation; names that matched by pattern or phonetics were checked to confirm matching. Unmatched names were queried manually in WoRMS using the truncated epithet, as described above.

Names for which no match could be identified in WoRMS were searched online in Google Books, Google Scholar, and the Zoological Record to determine their status as valid or synonym. If no treatment since 1950 was found, or if sources conflicted as to status, with one not clearly more reliable than another, I assigned a status of *nomen dubium* or *taxon inquirendum*. If no treatment whatsoever was found, I considered the name a manuscript (unpublished) name.

ANSP does not yet have a standardized bivalve inventory so to estimate completeness of bivalves in WoRMS I queried the main collection database to generate a list of lots by name. I sorted the list by epithet within each bivalve family to group variant spellings. From this list I chose 100 rare nominal species, deliberately avoiding well known groups such as the Cardiidae and Pectinidae and well-covered geographic areas. Their names were evaluated in the same way as names of gastropods.

The number of named terrestrial pulmonate species was estimated by totaling the stated minimum and maximum estimates of species diversity for each genus-group taxon treated by Schileyko (1998–2007). Results were summed by family and compared to tallies of species listed as valid in various published treatments. The number of named terrestrial

operculate species was estimated from the average completeness of the ANSP collection for terrestrial taxa, which in turn was estimated from the collection inventory by querying for the number of species in each family and comparing it to the published estimates of diversity.

I have used "recent" in the sense of "extant in the last 500 years", rather than "Holocene". Species known to have gone extinct during that period are included in the totals reported here, although their exclusion would not have a significant effect on the overall estimate of diversity, there being fewer than 600 historical extinctions of mollusks documented thus far (Régnier *et al.* 2009). In discussing higher taxa, I have used a mixture of clades (*e.g.*, Neogastropoda) and grades (*e.g.*, Ptenoglossa) for ease of reference.

RESULTS

Marine Mollusca

On 25 October 2013, WoRMS contained 43,696 accepted species of Mollusca, according to its summary statistics page. The totals stated for component taxa of Mollusca in the WoRMS taxon tree totaled 43,699 (Table 1). This slight discrepancy probably results from WoRMS doing summary calculations on a live database, in which entries might change or be added while the calculations are being done.

The WoRMS summary statistics are supposed to exclude species that are not recorded as marine or brackish (*i.e.*, terrestrial or freshwater) and those that are fossil only. Table 1 shows how many species are excluded in each category by taxon. The WoRMS summary figures by taxon (Table 1) compare well with those directly queried. The main difference is in counts of species that are freshwater and brackish, but not marine. WoRMS includes them; I have excluded them if they are part of predominantly freshwater radiations (*e.g.*, Hydrobiidae) and included them if they are part of mainly marine radiations (*e.g.*, Teredinidae). Relative to the counts in WoRMS (43,699), about 220 species are excluded, giving a total of 43,480.

Erroneous listings

Next, I estimated the prevalence of duplicate names and other errors that inflate the count of species (Table 2). I found by random sampling that among unverified names for gastropods (n = 4,096) about 5.5 ± 2.3 % were erroneous, compared to 24 ± 6% for bivalves (n = 222). Among verified names, about 2.5 ± 1.1% for gastropods and 2.0 ± 1.4% for bivalves were erroneous. Based on the standard errors, these percentages suggest that incorrect listings inflate the totals for gastropods by 937 ± 328 species and for bivalves by 210 ± 111 species. Duplicates were also found in the minor classes by taking a complete list of accepted species in each class and sorting by specific epithet, but these were minor in effect (39 duplicates, 1.4% across minor classes). Altogether, erroneous listings inflate the numbers by about 3% and the total in WoRMS should be adjusted from 43,480 to 42,294 ± 346 species. See Appendix 1, Supplementary Documents (http://www.bioone.org/doi/suppl/10.4003/006.032.0204/suppl_file/Rosenberg_2014_suppl.xlsx) for a list of the names sampled.

Missing names

In the random samples from the ANSP collection of 200 names of gastropods in different abundance classes, the percentage of names missing from WoRMS increased with the rarity of the name, with more than 10% missing in the rarest group, but when only valid names (Table 3, Fig. 2) were considered, there was not a significant difference among the 5 classes (chi-square, 8.231; p = 0.0835). Regrouping the data into two classes ("rare", 1 and 5 lots and "common", 10, 20+ and 40+ lots), did give a significant chi square (6.981; p = 0.0082). The chi-square calculations took into account that N differed slightly among the frequencies classes (see Table 3). It was less than 200 in some cases because I excluded sampled names that proved to be outside of scope for WoRMS (manuscript, fossil, or terrestrial) or that were "double hits"—different names from the ANSP collection that were synonyms of the same name in WoRMS and thus not independent tests for missing names.

The selected sample of bivalve names (purposely biased toward rare names) returned values consistent with the rarest two size classes for gastropods (Fig. 2), but not the commoner size classes, in terms of the percentage of names missing from WoRMS. With all data pooled, 2.75 ± 0.50% (*SE*) of the sampled lots represent valid species that were missing from WoRMS, so 1,086 ± 198 should be added to the total estimated in Table 2. This gives an estimate of 43,380 ± 398 species for total marine diversity (Table 4). With data separated into rare and common species (Table 3), an overlapping estimate of 43,610 ± 465 results (Table 4). I have used the latter estimate in subsequent calculations herein. See Supplementary Documents (http://www.bioone.org/doi/suppl/10.4003/006.032.0204/suppl_file/Rosenberg_2014_suppl.xlsx) for a list of the gastropod (Appendix 2) and bivalve names (Appendix 3) sampled and their statuses.

Table 5 shows the gastropods species selected from the ANSP collection distributed by taxonomy, with the percentage of names missing from WoRMS. Figure 3 shows that only Opisthobranchia and Pulmonata are likely to exceed 5% missing from WoRMS. Table 6 shows that some taxa differ significantly from the even distribution expected between the abundance classes, indicating that selecting species randomly with respect to abundance (number of lots) does not result in random selection with respect to

Table 1. Species diversity by taxon from queries in the World Register of Marine Species (WoRMS). "WoRMS summary" = species tallies from WoRMS taxon tree; "species accepted" = accepted taxa of species rank with no other restriction; "unverified" = status as accepted not verified by taxonomic editor; "> 1 June 2012" = growth of database from addition of newly described species after that date; "quarantined" = names formally quarantined in WoRMS as problematic (*e.g.*, Stuardo manuscript names in Bivalvia) or of unknown status; "fossil only" = not recent; "not marine" = freshwater only, terrestrial only, or brackish and freshwater with clade primarily freshwater; "revised total" = species accepted minus quarantined, fossil only and not marine, adjusted for any overlaps among those categories.

Taxon	WoRMS summary	Species accepted	Unverified	> 1 June 2012	Quarantined	Fossil only	Not marine	Revised total
Gastropoda								
Patellogastropoda	328	335	69	0	0	7	0	328
Vetigastropoda	3,425	3,435	555	79	0	11	0	3,424
Cocculiniformia	49	49	0	0	0	0	0	49
Neomphalina	44	44	0	0	0	0	0	44
Neritomorpha	200	208	26	0	0	0	8	200
Caenogastropoda								
Abyssochrysoidea	34	34	0	0	0	0	0	34
Campaniloidea	15	15	0	0	0	0	0	15
Cerithioidea	593	675	123	4	0	0	84	591
Cyclophoridea	1	1	0	0	0	0	1	0
Epitonioidea	772	774	513	3	0	3	0	771
Eulimoidea	1,005	987	375	33	0	7	0	980
Triphoroidea	1,388	1,391	46	102	0	3	0	1,388
Viviparoidea	3	7	3	0	0	0	7	0
Littorinimorpha	5,083	5,447	801	22	0	27	389	5,031
Neogastropoda	12,578	12,598	907	262	0	113	2	12,483
Heterobranchia								
non-pulmonate	6,989	7006	611	42	2	12	15	6,977
Pulmonata	268	449	67	13	0	0	195	254
Subtotal, Gastropoda	32,775	33,455	4,096	560	2	183	701	32,569
Bivalvia	8,090	8,275	222	73	89	58	50	8,078
Cephalopoda	832	835	239	1	3	1	0	831
Polyplacophora	989	989	6	0	0	0	0	989
Aplacophora								
Caudofoveata	132	132	0	0	0	0	0	132
Solenogastres	273	273	0	4	0	0	0	273
Monoplacophora	31	31	0	1	0	0	0	31
Scaphopoda	577	579	0	2	1	1	0	577
Total	**43,699**	**44,569**	**4,563**	**641**	**95**	**243**	**751**	**43,480**

taxonomy. Neotaenioglossa is biased toward higher abundance and Ptenoglossa and Heterostropha are biased toward lower abundance.

Terrestrial diversity

Summation of stylommatophoran diversity from Schileyko (1998–2007) showed 17,575 to 18,613 species-group taxa. Schileyko's counts often combined species and subspecies, however, and so could be inflated. To test this, I compared his figures to those reported in various species catalogues published over the last 35 years (Table 7). Those catalogues treated 34 families and listed 11,116 species, 10% more than the higher end of Schileyko's estimate, corresponding to about 20,500 species for all stylommatophorans.

The inventory of the ANSP collection recorded 10,021 stylommatophoran species, excluding Cerionidae (see Discussion) and slugs that lack external shells (since the inventory currently does not cover the alcohol preserved collection). In the families compared in Table 7, ANSP holds 5,844 species. It is therefore between 50.2% (10,021/19,979) and 61.5% complete (5,844/9,495) for described stylommatophoran species. The 2,323 terrestrial operculate species inventoried in the ANSP collection thus extrapolate to 3,777 to 4,627 species worldwide, if they have the same proportional completeness as the

Table 2. Counts of species recognized as valid in WoRMS, adjusted for duplicate and extralimital listings (*e.g.*, freshwater, terrestrial, and fossil only not flagged as such). "June 2012" and "Oct. 2013" = species counts as of those dates; "new spp." = species named after 2011 added after 1 June 2012; "growth w/o new" = increase (or decrease) in valid species between June 2012 and Oct. 2013 from addition of species previously missed, changes in synonymy and correction of errors; "unverified" and "verified" refer to whether a listed species was verified by a taxonomic editor; "wrong" = percentage of erroneous listings; "*SE*" = standard error of the percentage; "adjusted" = estimate of valid species using upper and lower bounds based on the standard errors of percentage wrong.

					Unverified			Verified		
Taxon	**June 2012**	**Oct. 2013**	**new spp.**	**growth w/o new**	**total**	**wrong**	***SE***	**wrong**	***SE***	**Adjusted ± *SE***
Gastropoda	28,861	32,569	560	10.9%	4,096	5.5%	2.28%	2.5%	1.1%	31,632 ± 328
Bivalvia	7,825	8,078	73	2.3%	222	24%	6.04%	2.0%	1.40%	7,868 ± 111
Cephalopoda	821	831	1	1.1%	239	4.2%	–	1.2%	–	814 ± 0
Polyplacophora	972	989	0	1.7%	6	100%	–	1.1%	–	972 ± 0
Aplacophora	402	405	4	-0.2%	0	–	–	0.2%	–	404 ± 0
Monoplacophora	30	31	1	0.0%	0	–	–	0.0%	–	31 ± 0
Scaphopoda	577	577	2	-0.3%	0	–	–	0.7%	–	573 ± 0
Total	**39,488**	**43,480**	**641**	**8.5%**	**4,563**	**6.5%**		**2.3%**		**42,294 ± 346**

stylommatophorans at ANSP. This seems a reasonable assumption based on the Annulariidae, the only major operculate family for which a current revision is available. Watters (2006) recognized 669 to valid 692 species of annulariids; ANSP holds 399 of these (57.7% to 59.6%), following Watters synonymies.

DISCUSSION

Marine Mollusca

Analysis of the WoRMS database shows that the estimated number of species missing from WoRMS, about 1,200 species is essentially the same as the number of erroneous and duplicate listings that inflate the totals (as of October 2013): about 1300 species. The total found by querying WoRMS, 43,480 is the similar to the total after subtracting errors and adding missing species: 43,600 ± 465. Converting the standard error to a 95% confidence interval (multiplying by 1.96) gives an overall estimate of 43,600 ± 900 named marine mollusk species.

Duplicates were higher in bivalves because most verified names were imported at one time from Huber (2010, CD-ROM), and some preexisting unverified names in WoRMS were not checked against them. More surprising was that 2.5% of verified names in gastropods, and 2% in bivalves were erroneous, despite having been vetted by a taxonomic

Table 3. Percentages of names missing from WoRMS based on sampling the ANSP collection inventory by frequency classes for gastropods and for selected rare bivalves (see methods). "All pooled" combines data for gastropods and bivalves; "rare" combines data from gastropods with 1 and 5 lots with data from bivalves; "common" combines data from gastropods with 10 or more lots. *N* is less than 200 for some gastropod groups due to exclusion of unavailable (manuscript or nude), extralimital (non-marine or fossil only) and duplicate names.

		Missing names			Missing valid names		
Group	***N***	**Total**	**%**	***SE***	**Total**	**%**	***SE***
Gastropods, 1 lot	194	22	11.3%	2.3	7	3.6%	1.3
Gastropods, 5 lots	198	14	7.1%	1.8	10	5.1%	1.6
Gastropods, 10 lots	199	10	5.0%	1.5	4	2.0%	1.0
Gastropods, 20+ lots	199	5	2.5%	1.1	3	1.5%	0.9
Gastropods, 40+ lots	200	4	2.0%	1.0	2	1.0%	0.7
Rare bivalves	100	8	8.0%	2.7	4	4.0%	2.0
All pooled	1090	62	5.69%	0.70	30	2.75%	0.50
Rare (gastropods + bivalves)	492	44	8.90%	1.29	21	4.27%	0.91
Common (gastropods)	598	18	3.01%	0.70	9	1.51%	0.50

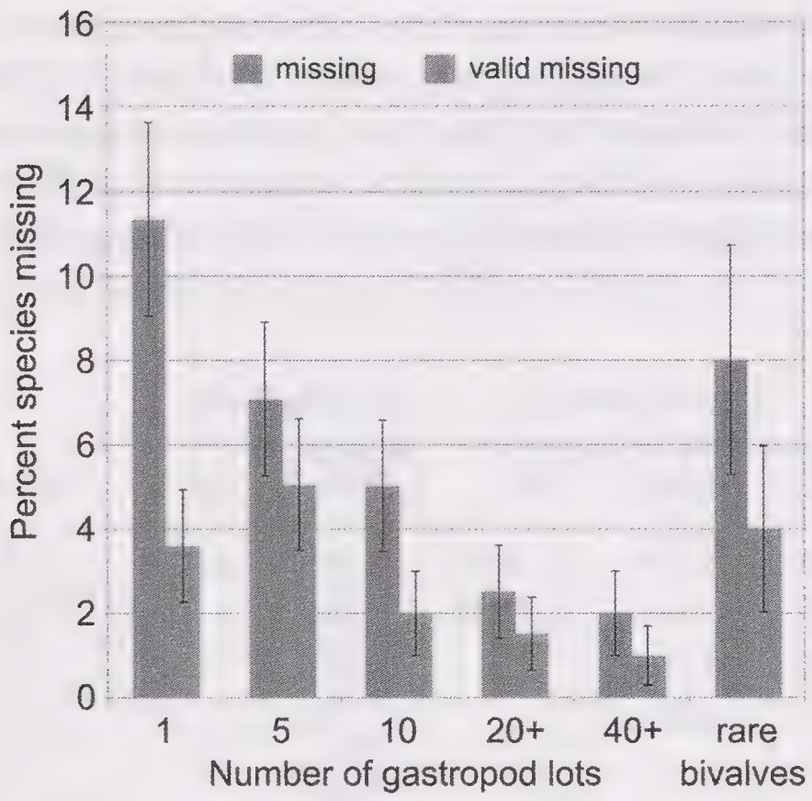

Figure 2. Percentage of names randomly sampled from ANSP collection by abundance classes (1 to 40+ lots) that are missing from WoRMS, comparing all missing names to valid missing names. Error bars show standard errors. Names missing among rare bivalves selected from the ANSP collection are shown from comparison. Data shown in Table 3. (Color shown in electronic version only).

editor. Across verified and unverified names the most common error was listing a name as valid in two different genera, but I found instances of names referring to taxa that were non-marine, fossil only, synonymous, dubious, and taxon inquirendum and in one case non-existent (these are detailed in the Appendix 1, Supplementary Documents, http://www.bioone.org/doi/suppl/10.4003/006.032.0204/suppl_file/Rosenberg_2014_suppl.xlsx).

The estimate of 43,600 marine species is substantially lower than that of Bouchet (2006): 52,525 species (which I agreed with at the time), based on summing estimates across "essentially non-overlapping" geographic regions. The total from his footnote 18 is actually 54,269 as North Pacific (1,744) was omitted. Including the North Pacific species along with the 3,800 marine species named from 2006 to October 2013 (queried in WoRMS), Bouchet's estimate corresponds to about 58,000 species, 33% higher than estimated herein. Which estimate is correct determines which marine phylum is most diverse: arthropods are currently listed as having 56,000 species in WoRMS.

Bouchet's estimate has two main uncertainties: the size of the Indo-Pacific fauna and the degree of overlap with other regions, which was not accounted for. Bouchet considered that the Indo-Pacific molluscan database (IPDB) (Rosenberg et al. 2002) was about two-thirds complete, and thus extrapolated from its total of 24,269 to a figure of 32,000 species. To estimate completeness, I took a random sample of 200 of the 1,000 gastropods names from Table 3 and assigned them to ocean regions, finding 103 from the Indo-Pacific. (A second random sample was needed because I had not saved the random numbers of the original selection.) Of these, 18 were missing from IPDB, including 8 valid species, which corresponds to 7.8 ± 2.6 % missing, a lower percentage than any of the principals of IPDB had thought likely. This percentage missing yields an adjustment to 26,000 rather than 32,000 species.

The other issue is overlap between ocean regions. IPDB includes information on other regions that Bouchet tallied. It records 593 species from New Zealand, 1293 from South Africa (1137 tropical and 224 temperate, with some overlap), and 213 from the Eastern Pacific. (I compiled these using the "Browse Geographic Regions" feature of the website and removed duplicates and non-species level taxa manually.) IPDB also contains a large portion of the North Pacific fauna, by virtue of an import of data from Higo, Callomon and Goto (1999) for Japan. It cannot be readily queried to parse out the temperate species, as many were not given geographic flags, but if one-third of the north Pacific fauna is in northern Japan, then there is an overlap of about 600 species with IPDB. The Western Atlantic fauna has 21.7% overlap with the fauna of other regions (query of Malacolog 4.1.1, Rosenberg 2009), which corresponds to 1,339 out of 6,170 species listed by Bouchet. There is also overlap between the West African fauna and the European and South African faunas, which, if taken as 20%, represents 500 species. Summing up these various overlaps yields a total of 4,538. There are additional overlaps: North Pacific with European, and Antarctic and

Table 4. Total number of marine mollusks including estimate of species missing from WoRMS, based on adjusted values from right-most column in Table 2, with minor classes totaling 2,794. The first calculation uses the pooled value for percentage missing from Table 3; the second assumes rare taxa are more likely to be missing from WoRMS than common taxa and uses the corresponding percentages from Table 3. The total number of gastropods plus bivalves is parsed into rare vs. common in the ratio 66% to 34% observed in the ANSP for species with ≤ 7 lots and ≥ 8 lots. Standard errors were propagated as the square root of the sum of squares across columns and by addition within columns.

Group	WoRMS adjusted	Missing %	Missing	Total	Plus minor classes
Gastropoda + Bivalvia	39,500 ± 346	2.75 ± 0.50%	1086 ± 198	40,586 ± 398	43,380 ± 398
Common	13,430 ± 118	1.51 ± 0.50%	203 ± 67	13,633 ± 136	43,610 ± 465
Rare	26,070 ± 228	4.27 ± 0.91%	1113 ± 228	27,183 ± 329	

Table 5. Gastropod names from Table 3 regrouped to show percentage missing from WoRMS by taxonomy; *N* = number of species sampled. Opisthobranchia is used in a broad sense to include Acteonidae and Ringiculidae (2 species of each); Heterostropha contains the rest of the lower Heterobranchia (mainly Pyramidellidae and Architectonicidae); Pulmonata includes Ellobiidae, Siphonariidae and Amphibolidae. One heteropod and one stylommatophoran (miscoded as marine in the ANSP taxonomic dictionary) are not shown. The arrangements of patellogastropods and some ptenoglossans (Triphoridae) in the ANSP collection were updated against WoRMS in 2012 before work on this manuscript began, so the percentage missing from WoRMS may be artificially low for those taxa, however, the overall effect is minor, since only 1 or 2 names would be involved given the low *N* for those taxa.

		Missing names			Missing valid names		
Group	***N***	**Total**	**%**	***SE***	**Total**	**%**	***SE***
Patellogastropoda	26	0	0	0	0	0	0
Vetigastropoda	123	11	8.9%	2.6	5	4.1%	1.8
Neritogastropoda	6	2	33.3%	19.2	2	33.3%	19.2
Neotaenioglossa	207	9	4.3%	1.4	3	1.4%	0.8
Ptenoglossa	48	1	2.1%	2.1	1	2.1%	2.1
Neogastropoda	484	15	3.1%	0.8	8	1.7%	0.6
Heterostropha	41	1	2.4%	2.4	1	2.4%	2.4
Opisthobranchia (*s.l.*)	36	8	22.2%	6.9	3	8.3%	4.6
Pulmonata	15	5	33.3%	12.2	3	20.0%	10.3

Magellanic with New Zealand; also some species in IPDB have distributions including South Africa or New Zealand that are not flagged. I therefore use 5,000 species as an overall estimate of the degree of overlap across the oceanic regions.

Combining this overlap with 6,000 fewer Indo-Pacific species (32,000–26,000), gives a revised estimate of 47,000 marine mollusk species (58,000–11,000) based on the adjusted Bouchet data. This is still 3,400 higher (7.4%) than estimated herein. As with the WoRMS database, IPDB has some known duplication and also includes some non-marine taxa, but this seems to have been taken into account: the IPDB website lists 28,357 species "in current use" as of May 2006, about 4,000 more than the base Bouchet used. Therefore, either IPDB has additional, unrecognized duplication, the degree of overlap among faunas is greater than estimated above, the WoRMS database is missing more taxa than estimated above, or the situation is some combination of these possibilities.

All of the 26 species missing from WoRMS identified by randomly sampling the ANSP collection are from the Indo-Pacific, but only 52% (103/200) of the sample was from the Indo-Pacific. Of the non-valid missing names (synonyms and alternate combinations) 39% were not Indo-Pacific: Eastern Atlantic (16), Western Atlantic (12) and Eastern Pacific (23), versus Indo-Pacific (80). This reflects the prioritization of entry of valid names over synonyms by the WoRMS editors in order to reach an estimate of molluscan diversity. The random sampling done herein encompassed all ocean regions, but found gaps for valid names only in the Indo-Pacific. Overall, WoRMS is missing about 3% of marine mollusk species (1,300/43,600), with the main gaps in the Indo-Pacific. If that fauna comprises 50% of marine mollusks, then about 6% of Indo-Pacific mollusk species are still missing from WoRMS. IPDB is currently being merged to WoRMS, which will fill in some missing species.

A major assumption in my analysis is that the ANSP collection and WoRMS do not have correlated weaknesses. Suppose that a particular family has 1,000 species, but ANSP and WoRMS each have only 200 names in that family. At random one would expect 40 names in common (20% of 200), but collections are surely biased toward common species, and a literature database might also have the same bias: common species are cited more often so there are more ways to encounter them to include them in the database. If such correlation led to there being 80 species in common within the target family instead of 40, the estimated percent missing from WoRMS would be 60% (120/200) instead of 80%.

Figure 2 shows that rare species (those in the lower abundance classes) are indeed more likely to be missing from WoRMS and Table 4 shows that when this is taken into account, the estimate of diversity is higher, but not by a significant amount. The rarest species, those represented by only 1 lot at ANSP, actually have a lower percentage missing from WoRMS (3.6%) than the next rarest class (5 lots, 5.1%), but the difference is not significant (Table 3, Fig. 2). The trend is interesting, however, because it suggests that there is not a separate class of ultra-rare species that would throw off estimates of diversity. Rather, there is a distinction between nominal species and valid species. Nominal species represented by only 1 lot in the ANSP collection are more likely to be spurious: dubious names, or synonyms not flagged as such. (Manuscript names are also spurious, but they are not

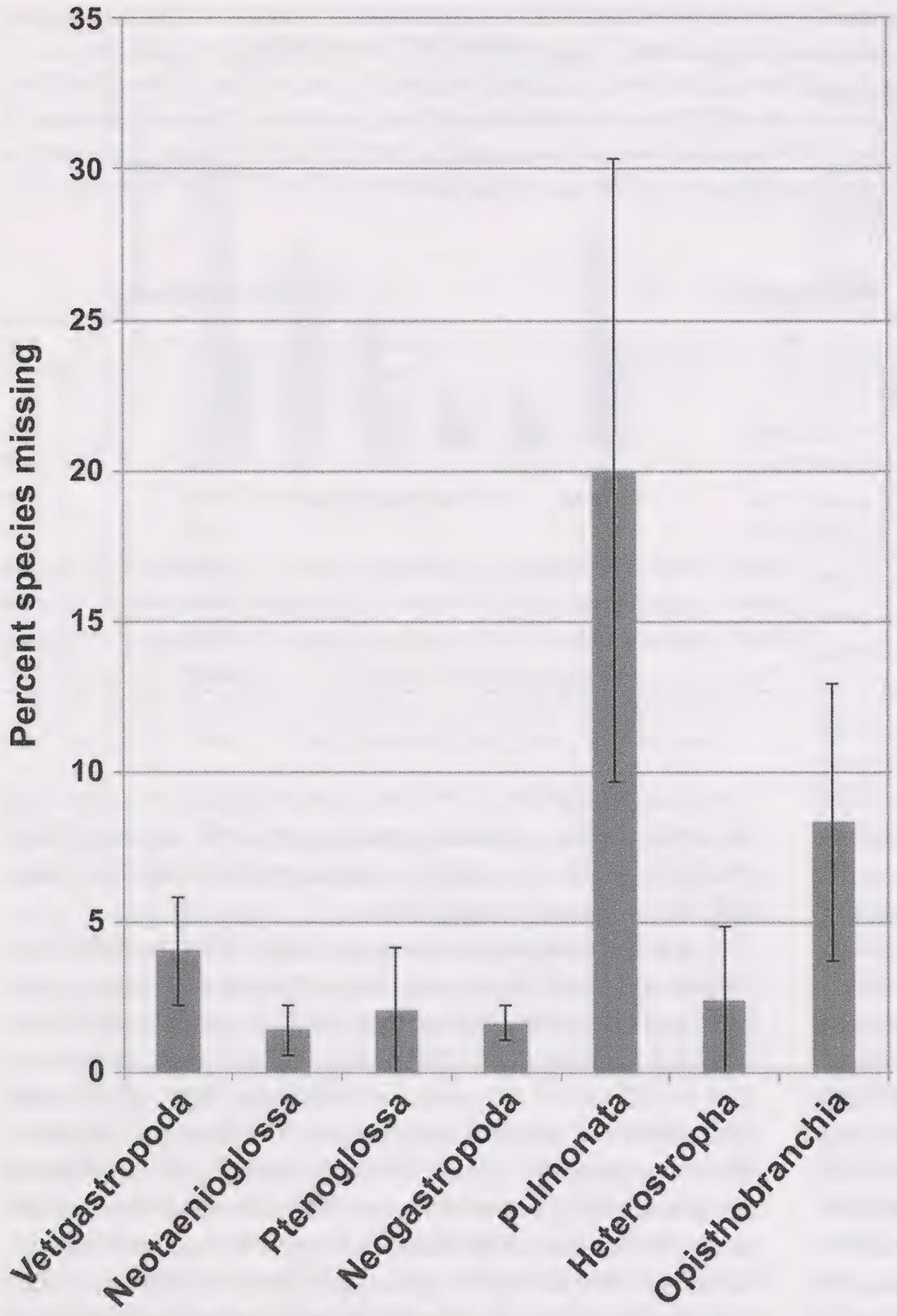

Figure 3. Percentage of names randomly sampled from ANSP collection missing from WoRMS by group (clade or convenient grade). Patellogastropoda not shown as no missing names were found; Neritogastropoda not shown as sample too small to be meaningful. Error bars are standard errors. Data shown in Table 5. (Color shown in electronic version only).

available names and so are not nominal species; they were excluded from figures and calculations herein, as noted above.) Nominal species represented by five lots have generally come into the collection from several sources, so their names are more likely to represent valid species. Names that are seldom cited are less likely to represent valid species, and are more likely to be missing from WoRMS, which has prioritized the entry of valid names. Also, rare names are less likely to be correlated between databases and collections and so are less likely to mislead random sampling.

Random sampling of the ANSP inventory by abundance did not lead to random sampling by taxonomy (Table 6). Chi square tests showed significant departures from null distributions for three taxa, with Neotaenioglossa biased toward higher abundance classes and Heterostropha and Ptenoglossa (Epitonioidea, Eulimoidea, Triphoroidea) biased toward lower abundance classes. This may reflect a biological signal as many neotaenioglossans are herbivorous and therefore expected to have higher abundance because of lower trophic level, whereas ptenoglossans are generally parasitic, with lower abundance because of their higher trophic level. Despite this pattern, neither Ptenoglossa nor Heterostropha had a significantly higher proportion of species missing from WoRMS than expected (Figure 3). The greatest proportions of missing species were seen in Neritogastropoda and marine pulmonates, but these are both relatively low diversity groups, so their large error bars (Table 5) add little uncertainty to the estimate of diversity.

The best known group of gastropods in terms of species diversity is certainly the Neogastropoda, with recent treatments and catalogues by Tucker (2004, Turridae *sensu lato*), Snyder (2003, Fasciolariidae), Cossignani (2006, Marginellidae), Petit and Harasewych (2005, Cancellariidae); and Sterba (2004, Olividae), and unpublished lists by R. Houart on Muricidae, K. Monsecour on Columbellidae and K. Fraussen on Buccinidae all incorporated into WoRMS. I estimate that WoRMS is missing only 1.7 ± 0.6% (Table 5) of neogastropods. Neotaenioglossa, Ptenoglossa and Heterostropha are not significantly different from Neogastropoda in percentage of species missing (overlapping errors bars in Fig. 3), so WoRMS is generally very complete for high diversity groups of gastropods. The exception is Opisthobranchia with 8.3 ± 4.6 % missing. This percentage applies only to shelled opisthobranchs, however, as the ANSP inventory has not been extended to the alcohol collection as yet.

To assess the completeness of nudibranchs in WoRMS, I used listings in IPDB. IPDB doesn't have "Nudibranchia" in its taxonomic hierarchy, instead linking families directly to Opisthobranchia, so there was no quick way to do random sampling. Also, only in the Opisthobranchia, IPDB uses "Described" in the subgenus field to flag named species. I therefore searched for "Described" to get a list of Opisthobranch genera and took all species in nudibranch genera within those, alphabetically from A through G, getting a sample of 553 names. I eliminated nomenclatural duplicates from this list manually, leaving 528 names. Combining

Table 6. Distribution by frequency class for gastropod names from Table 3. Chi square with 4 degrees of freedom, two-tailed t-test, significant *p* values marked with asterisk. Random selection by number of lots does not result in random selection by taxonomy, which would give an even distribution.

Group	1 lot	5 lots	10 lots	20+ lots	40+ lots	Chi squared	*p* value
Patellogastropoda	3	6	6	7	4	2.077	0.722
Vetigastropoda	22	23	26	30	22	1.919	0.751
Neotaenioglossa	39	32	32	43	61	13.749	**0.008***
Ptenoglossa	17	14	9	1	6	16.167	**0.003***
Neogastropoda	82	96	112	104	90	5.669	0.225
Heterostropha	14	13	6	3	5	12.049	**0.017***
Opisthobranchia (*s.l.*)	10	7	6	8	5	2.056	0.726
Pulmonata	5	5	2	1	2	4.667	0.323

automated matching through the WoRMS portal and searching names in McDonald (2009), I determined that 59 of these represented valid species that were missing from WoRMS. In 61 cases one of the 528 names mapped to the same valid name as another. I excluded these as duplicates, so the percent valid names missing from IPDB is 12.6% [59/(528–61)]. Assuming that 60% of the 2121 nudibranchs in WoRMS are Indo-Pacific, about 160 are missing (2121*0.126*0.6). Assuming that no more than 2% are missing from the rest of the world, 180 are missing overall. About 60 of these are accounted for in the calculations in Table 4, so the overall effect on the estimate of global marine molluscan diversity is small. The overall percentage of nudibranchs missing (8.5%; 180/2121) is quite similar to the figure for shelled opisthobranchs, 8.3% (Table 5).

Another group which the ANSP inventory does not yet cover is Bivalvia, so I estimated its completeness by selecting 100 rare species as described in Methods. They appear to be drawn from the same distribution as rare gastropods, with 8 names missing, 4 of them valid (Fig. 2), so I combined data from gastropods and bivalves in estimating overall diversity. In my presentation of preliminary data for this study at AMS in 2012, I noted that the gastropod to bivalve ratio seemed to increase with the number of faunal provinces included, with Keen (1971) showing 3.0: 1 for the tropical Eastern Pacific, Higo, Callomon and Goto (1999) 3.4: 1 for Japan, which spans tropical temperate and boreal, and Rosenberg (2009, Malacolog) 3.9: 1 for the Western Atlantic (Greenland to Antarctic). This suggested that gastropods have smaller geographic ranges on average than bivalves. (I have since found that Nicol (1969) estimated this ratio as nearly 3.2 to 1, across various regional faunas.) Since the ratio for gastropods to bivalves in WoRMS was then 3.7: 1, I predicted that it would increase as WoRMS became more complete. Currently the ratio is 4.02: 1 (data from Table 2), suggesting that WoRMS may be reaching an equilibrium level, with completeness of gastropods and bivalves now similar. The same kind of analysis applied to the percentage of Neogastropoda among Gastropoda also suggests that WoRMS is nearly complete. In June 2012, WoRMS had 41.6% Neogastropoda, which is higher than in other large-scale works: Abbott (1974) 36.9% (1657/4490); Keen (1971) 37.2% (900/2421); Higo, Callomon and Goto (1999) plus Okutani (2000, for shell-less); 38.5% (2015/5235); and Rosenberg (2009), 39.6% (2047/5167). In the current study the percentage has dropped to 38.3%, which is within the range of the other works, as coverage of non-neogastropods has strengthened.

The minor classes are essentially complete in WoRMS, with Aplacophora and Scaphopoda showing slight decreases when newly described species are discounted (Table 2, "growth w/o new"), reflecting synonymization of species formerly recognized as valid. The flux of species in and out of synonymy will be an ongoing source of uncertainty in estimates of molluscan diversity. There are surely species currently listed as valid in WoRMS for which a published synonymization has been overlooked. Also, some recently named species will be prove to be synonyms: the apparently acceleration of naming reflected by the upswing in the naming curve since about 1990 (Fig. 1) is at least partially an artifact of insufficient time having passed for taxonomic revisions to reveal synonyms. Of 4,674 marine species named in the last ten years (2004–2013), 94 (2%) have already been synonymized (query of WoRMS). Balancing this effect to an unknown degree will be the removal of earlier named taxa from synonymy. The errors bars on my estimate of marine diversity do not account for the flux of synonyms.

While it is not currently possible to adjust the overall estimate of marine molluscan diversity to take into account this flux (which would require knowing an average lag time between original description and relegation to synonym), there is reason to believe the figure of 43,600 is not an underestimate: many species listed in WoRMS as accepted are actually *nomina dubia*. These are taxa that have not been treated as valid in many years, and many have never been reevaluated since they were named. For example most of the more than 200 pyramidelloid taxa named by Saurin (1958, 1959, 1962) are listed as accepted

Table 7. Stylommatophoran species diversity by family summed across the low and high estimates for genus-group taxon stated by Schileyko (1998–2007). "Other" shows species diversity from the listed reference. At the bottom "Families compared" gives the sum for families with data in the "other" column; this was also calculated excluding slugs for comparison to the ANSP inventory. The number in brackets at bottom right is the extrapolation of the sum to all families.

Family	Low	High	Other	Reference	Family	Low	High	Other	Reference
Bulimulidae	1754	1874	1493	Richardson 1995	Milacidae	43	44		
Clausiliidae	1331	1387	1278	Nordsieck 2007	Humboldtianidae	40	41	42	Richardson 1982
Camaenidae	1040	1073	1073	Richardson 1985	Athoracophoridae	38	40		
Ariophantidae	992	1034			Discidae	38	44		
Urocoptidae	991	1014	931	Richardson 1991	Epiphragmophoridae	37	38	61	Richardson 1982
Bradybaenidae	827	873	898	Richardson 1983	Strophocheilidae	34	34		
Subulinidae	802	827			Helicodontidae	30	37	65	Richardson 1980
Achatinellidae	631	654			Haplotrematidae	29	32	21	Richardson 1989
Streptaxidae	623	657	1127	Richardson 1988	Daudebardiidae	28	29		
Charopidae	532	545			Dorcasiidae	27	27		
Hygromiidae	511	557	1147	Richardson 1980	Truncatellinidae	26	27		
Endodontidae	440	457			Strobilopsidae	24	26		
Helicidae	396	433	606	Richardson 1980	Thysanophoridae	22	29	90	Richardson 1989
Zonitidae	381	408			Gymnarionidae	21	21		
Euconulidae	364	395			Helicodiscidae	21	24		
Amastridae	321	326	331	Solem 1990	Cochlicellidae	21	25	21	Richardson 1980
Oleacinidae	311	327			Anadenidae	19	21		
Enidae	301	340			Cochlicopidae	18	23		
Achatinidae	269	277			Parmacellidae	17	17		
Polygyridae	260	285	239	Richardson 1986	Monadeniidae	17	19	13	Richardson 1982
Vertiginidae	240	263			Philomycidae	15	22		
Chronidae	236	249			Spelaeodiscidae	13	14		
Helicarionidae	206	227			Caryodidae	12	12		
Pleurodontidae	186	203	220	Richardson 1985	Clavatoridae	12	12		
Helminthoglyptidae	177	182	206	Richardson 1982	Corillidae	12	12	11	Richardson 1986
Ferussaciidae	177	190			Ryssotidae	12	14		
Rhytididae	172	172	199	Richardson 1989	Sculptariidae	10	10	16	Richardson 1986
Orculidae	150	170			Megalobulimidae	10	10		
Partulidae	137	139	142	Richardson 1990	Chlamydephoridae	10	12	12	Richardson 1989
Succineidae	135	141			Oopeltidae	10	12		
Trochomorphidae	124	138			Trigonochlamydidae	9	9		
Xanthonychidae	123	127	107	Richardson 1982	Sphincterochilidae	8	10	33	Richardson 1980
Pachnodidae	122	136			Ammonitellidae	7	8	9	Richardson 1989
Dyakiidae	109	111			Pyramidulidae	7	10		
Gastrocoptidae	106	116			Megaspiridae	6	6		
Pupillidae	100	105			Draparnaudiidae	6	6		
Chondrinidae	97	97			Aillyidae	5	6		
Punctidae	97	100			Testacellidae	5	7		
Acavidae	96	96			Cystopeltidae	4	4		
Glessulidae	90	90			Ostracolethidae	4	4		
Oreohelicidae	90	90	60	Richardson 1984	Cerionidae	4	5		
Vitrinidae	84	90			Staffordiidae	3	4		
Plectopylidae	82	82	109	Richardson 1986	Rhysotinidae	2	2		
Hypselostomatidae	72	79			Boettgerillidae	2	2		
Sagdidae	68	84	114	Richardson 1986	Elonidae	2	2		
Valloniidae	63	64			Unknown	2	3		
Systrophiidae	60	65	146	Richardson 1989	Macrocyclidae	1	1		
Gastrodontidae	57	60			Micractaeonidae	1	1		
Ciliellidae	56	64	84	Richardson 1980	Thyrophorellidae	1	1		

Table 7. (Continued)

Family	Low	High	Other	Reference	Family	Low	High	Other	Reference
Arionidae	54	66			Papillodermidae	1	1		
Agriolimacidae	47	50	123	Wiktor 2000	Bielziidae	1	1		
Orthalicidae	47	102	89	Richardson 1993	**Total**	**17,575**	**18,613**		[all-families estimate]
Limacidae	46	48			Families compared	9542	10,112	11,116	[20,467]
Spiraxidae	45	53			Same, without slugs	9495	10,062	10,993	

in WoRMS, but most have never been cited subsequently. Similarly, many names of pyramidellids are propagated on faunal lists (*e.g.*, Keen 1971, Abbott 1974), but have not been revised since they were named. WoRMS currently lists more than 1,000 accepted species in *Turbonilla* alone, thereby overtaking *Conus* as the most diverse molluscan genus (Kohn 1992), but unlike the situation in *Conus*, most of the species are poorly known. In contrast to the situation in Pyramidellidae, when names of Turridae from Tucker (2004) were entered into WoRMS, nominal taxa that had not been allocated to a modern genus were omitted. This uneven treatment of seldom-cited and poorly understood taxa adds uncertainty to estimates of molluscan diversity.

Non-marine Mollusca

Lack of an overall database for non-marine mollusks prevents a statistical treatment such as that I applied to the marine mollusks. For freshwater diversity I have accepted the two most recent rigorous tallies: the estimate of 3,795–3,972 freshwater gastropods from Strong et al. (2008) and the enumeration of 1209 freshwater bivalves by Graf (2013). This gives an overall total for freshwater mollusks of about 5,100 species (Table 8), which is substantially lower than the 7,000 estimated by Lydeard et al. (2004). I am, however, in substantial agreement with the latter's estimate of 24,000 species for terrestrial mollusks, having reached a total of 24,500 ± 2,000. (The error figure here is merely a range of likely values rather than a statistical confidence interval.)

Summing diversity from Schileyko's work gives a total of 17,575 to 18,613 stylommatophoran species (Table 7). The tallies from the species catalogues total 11,116, about 10%, more than the high-end total from Schileyko for the treated families. This extrapolates to 20,500 for all stylommatophorans. A bracket of 19,000 ± 1,500 species spans from the low-end total from Schileyko to 20,500. Even this bracket might be low: most of the nomenclators considered are by Richardson, who treated all subspecies as synonyms, whereas the trend in land snail systematics is to elevate subspecies to full species. In compiling information from Richardson, I recorded tallies genus by genus, mapping the genera to the families that Schileyko placed them in to control for different classifications. I excluded Richardson (1992) on Cerionidae, which, unlike his other catalogues, treated nominal taxa rather than valid taxa. Another factor is that Schileyko's totals are now an average of ten years old and Richardson's are 20–34 years old and many new species have since been named. To compensate for these effects, I shift the bracket upward by 1,000 species, to 20,000 ± 1,500 stylommatophoran species.

My estimate of terrestrial operculate diversity has two uncertainties. It is based on the percentage completeness of the ANSP collection for pulmonate species, which may not be a good estimator for operculate species. My field experience in Jamaica suggests that operculates have smaller geographic ranges on average than pulmonates, so they may tend to be rarer and therefore less well represented in collections. However, the percentage completeness of the operculate family Annulariidae in the ANSP collection, 57.7% to 59.6% is within the range of completeness of pulmonate groups (50.2–61.4%). The other uncertainty is in the assignment of some assimineids as terrestrial, freshwater or marine, however, the estimate of 4,200 ± 450 terrestrial operculate species should be broad enough to encompass this. The overall estimate of terrestrial diversity including non-stylommatophoran pulmonates, of which there are probably fewer than 200 valid species, is 24,500 ± 2,000 (Table 8).

Table 8. Recent Molluscan species diversity summed across estimates for marine, freshwater and terrestrial. Basis of estimates is discussed in the text, except for "Other terrestrial pulmonates". In Ellobiidae I estimated 40 Carychiinae (Weigand *et al.* 2011) and 10 Pythiinae that are not also marine and 130 Systellomatophora (Veronicellidae, Rathousiidae and Onchidiidae) (D. G. Robinson pers. comm.; Dayrat 2009). Total is rounded.

Group	Estimate
Marine mollusks	43,600 ± 900
Stylommatophora	20,000 ± 1500
Terrestrial operculates	4200 ± 450
Other terrestrial pulmonates	180 ± 50
Freshwater gastropods	3900 ± 100
Freshwater bivalves	1200 ± 50
Total	**73,000 ± 3000**

Overall Recent molluscan diversity

The overall total I estimate for described recent Mollusca, 70,000 to 76,000 species does not closely agree with any prior study and is lower than all recent estimates except that of Boss (1971). My previous estimate of 72,000 species (Rosenberg 1992) although within this range, does not match because many species have been named since then. If the naming patterns for freshwater and terrestrial taxa resemble those of marine taxa (Fig. 1), 72,000 species in 1992 extrapolates to 89,000 in 2013 (24% increase). Boss (1971, table 13) estimated 33,754 described species and 46,810 including undescribed species. He emphasized that many taxa have proven to have high synonym ratios when monographed, so for groups that had not been monographed recently he was conservative in estimating how many species might prove valid. However, many names in synonymy were not described as species but as varieties or forms, so the original hypothesis of the naming author was not that a species existed. In the Western Atlantic fauna, more than 60% of names introduced at the species rank are currently considered valid (query of Malacolog), so synonymy ratios must be used in the appropriate context.

If unrecognized synonyms and *nomina dubia* prove to constitute a substantial proportion of names currently treated as valid in molluscan species lists, mollusks may eventually lag behind chordates in terms of the number of valid species recognized. Currently, about 69,000 chordate species are recognized (Table 9), which is close to the lower end of my estimate for molluscan species. Also, naming rates for chordates are currently higher than for mollusks, about 750 species per year (Table 9), versus about 600 per year (467/year, 2004–2013, query of WoRMS, plus about 100 non-marine per year, query of Zoological Record), although the mollusks are generally regarded as having a higher level of undescribed diversity, as reflected in the many statements placing of total molluscan diversity at 200,000 species. The accelerating rate of chordate discovery is abetted by the accessibility of comprehensive databases of available names, which allows more rapid assessment of whether an unidentified taxon has been already named, and by molecular techniques, which are not yet as pervasive in malacology.

Lydeard et al. (2004) noted that mollusks have the highest documented extinction rate of any group of organisms, comprising 42% of the 693 extinctions documented on the IUCN Red List in 2002, versus 33% for tetrapods. While this is still true in relation to tetrapods, at the phylum level, chordate extinctions exceed molluscan extinctions on Red List 2013.2, with 325 (41 %) vs. 310 (39%). This is because of the inclusion of fish; tetrapods remain at 33%. (No tunicates or cephalochordates are listed by the IUCN.) Yet many molluscan extinctions are overlooked: as shown by Régnier et al. 2009, almost half of molluscan extinctions are not listed by the IUCN. Only 6,809 mollusk species have been assessed for the Red List and of these 27% (1,812) are listed as data deficient whereas 37,280 vertebrate species have been assessed, with 16% (5,908) data deficient. Thus 45% of vertebrates but only 7% of mollusks have a conservation status in IUCN.

Since 99% of molluscan extinctions are of non-marine taxa (Lydeard et al. 2004), development of master lists of described terrestrial and freshwater species is a high priority for molluscan conservation. The framework is now in place for "MolluscaBase": in February 2014 the data management staff at Flanders Marine Institute, which hosts WoRMS, reached an agreement with the Mollusca editors to broaden coverage of WoRMS to all Mollusca, recent and fossil. Such biotic databases are crucial for more rapid progress in molluscan systematics and conservation (Rosenberg 1997). Although documented molluscan species-level diversity is not as high as previously thought, undescribed diversity may exceed known diversity, as suggested by the species discovery curve in Figure 1, ongoing expeditionary work (Bouchet 2006) and molecular studies showing much overlooked diversity and regional endemism (*e.g.*, Meyer, Geller and Paulay 2005). In providing authoritative summaries of taxonomic, geographic

Table 9. Chordate species diversity and naming rates. Naming rate is based on a ten year average for tunicates, fish, amphibians and birds, and from Uetz (2010) for reptiles. Total for mammals was increased by 180 to account for 6 years of naming since tally.

Taxon	Species	Species/year	Source
Tunicata	3026	20	WoRMS
Cephalochordata	30	0	WoRMS
Fish	33,065	417	Catalogue of Fishes
Amphibia	7,215	180	http://amphibiaweb.org/amphibian/newspecies.html
Reptilia	9,909	100	http://www.reptile-database.org/db-info/SpeciesStat.html
Aves	10,518	8	IOUC http://www.worldbirdnames.org/
Mammalia	5,600	30	Reeder, Helgen and Wilson (2007)
Total	**69,363**	**755**	

and biotic information, online databases have an essential role to play in accelerating discovery and description of molluscan diversity.

ACKNOWLEDGMENTS

As editors of WoRMS, Philippe Bouchet, Serge Gofas and Bruce Marshall have been my partners in building the global list of marine mollusk species analyzed herein. Bouchet also provided an Excel file compiled by Claire Régnier of diversity by genus-group name in Schileyko (1998–2007). Paul Callomon provided a similar list of taxa in Schileyko, which I cross-linked to Régnier's list to check for missing taxa. Ira Richling (Staatliches Museum für Naturkunde, Stuttgart) patiently recruited manuscripts from symposium participants and managed the review process. Callomon, Richling, and an anonymous reviewer provided helpful comments on the manuscript. Richard Horwitz and Jerry Mead (ANSP) advised on statistics. David Robinson (USDA) advised on veroniceloid diversity. This research was based upon work supported by two grants: NIH IU01TW008163-01, Philippines Mollusk Symbiont International Cooperative Biodiversity Group (PI Margo Haygood, Oregon Health Sciences University), through a subcontract to Rosenberg, and by National Science Foundation DBI 1203605, for digital imaging of type specimens at the Academy of Natural Sciences.

LITERATURE CITED

Abbott, R. T. 1974. *American Seashells*, 2nd Edition. Van Nostrand Reinhold, New York, New York.

Boss, K. J. 1971. Critical estimate of the number of Recent Mollusca. *Occasional Papers on Mollusks* **3**: 81–135.

Bouchet, P. 2006. The magnitude of marine biodiversity. Pp. 31–64. *in*: C. M. Duarte, ed., *The Exploration of Marine Biodiversity: Scientific and Technological Challenges.* Fundación BBVA, Bilbao, Spain.

Chapman, A. D. 2011. *Numbers of Living Species in Australia and the World*, 2nd Edition. Australian Biological Resources Study, Canberra, Australia

Cossiginani, T. 2006. *Marginellidae and Cystiscidae of the World.* L'Informatore Piceno, Ancona, Italy.

Dayrat, B. 2009. Review of the current knowledge of the systematics of Onchidiidae (Mollusca: Gastropoda: Pulmonata) with a checklist of nominal species. *Zootaxa* **2068**: 1–26.

Filmer, R. M. 2001. *A Catalogue of Nomenclature and Taxonomy in the Living Conidae 1758–1998*. Backhuys, Leiden, Netherlands.

Graf, D. L. 2013. Patterns of freshwater bivalve global diversity and the state of phylogenetic studies on the Unionoidea, Sphaeriidae, and Cyrenidae. *American Malacological Bulletin* **31**: 135–153.

Groombridge, B. and M. Jenkins. 2002. *World Atlas of Biodiversity: Earth's Living Resources in the 21st Century.* University of California Press, Berkeley, California.

Higo, S., P. Callomon, Y. Goto. 1999. *Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan*. Elle Scientific Publications, Osaka, Japan.

Huber, M. 2010. *Compendium of Bivalves*. Hackenheim, Germany: ConchBooks. With CD-ROM.

Keen, A. M. 1971. *Sea Shells of Tropical West America*, 2nd Edition. Stanford University Press, Stanford, California.

Kohn, A. J. 1992. *A chronological taxonomy of Conus, 1758–1840.* Smithsonian Institution Press: Washington, DC.

Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Hershler, K. E. Perez, B. Roth, M. Seddon, E. E. Strong, and F. G. Thompson. 2004. The global decline of nonmarine mollusks. *Bioscience* **54**: 321–330.

Mayr, E. 1969. *Principles of Systematic Zoology*. McGraw Hill, New York, New York.

McDonald, G. R. 2009. *Nudibranch Systematic Index, Second Online Edition*. eScholarship: University of California. http://escholarship.org/uc/item/93c42364.

Meyer, C. P., J. B. Geller and G. Paulay. 2005. Fine scale endemism on coral reefs: archipelagic differentiation in turbinid gastropods. *Evolution* **59**: 113–125.

Nicol, D. 1969. The number of living species of mollusks. *Systematic Zoology* **18**: 251–254.

Nordsieck, H. 2007. *Worldwide Door Snails (Clausiliidae), Recent and Fossil*. ConchBooks, Hackenheim, Germany.

Okutani, T. 2000. *Marine Mollusks in Japan*. Tokai University Press, Tokyo, Japan.

Petit, R. E. and M. G. Harasewych. 2005. Catalogue of the superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia), 2nd Edition. *Zootaxa* **1102**: 1–161

Ponder, W., P. Hutchings and R. Chapman. 2002. *Overview of the Conservation of Australian Marine Invertebrates*. Environment Australia, Canberra, Australia.

Reeder, D. M., K. M. Helgen, and D. E. Wilson. 2007. Global trends and biases in new mammal species discoveries. *Occasional Papers, Museum of Texas Tech University* **269**: 1–35.

Régnier, C., B. Fontaine and P. Bouchet. 2009. Not knowing, not recording, not listing: Numerous unnoticed mollusk extinctions. *Conservation Biology* **23**: 1214–1221.

Richardson, C. L. 1980. Helicidae: Catalog of species. *Tryonia* **3**: iii, 697.

Richardson, C. L. 1982. Helminthoglyptidae: Catalog of species. *Tryonia* **6**: 117 pp.

Richardson, C. L. 1983. Bradybaenidae: Catalog of species. *Tryonia* **9**: ii + 253 pp.

Richardson, C. L. 1984. Oreohelicidae: Catalog of species. *Tryonia* **10**: i + 30 pp.

Richardson, C. L. 1985. Camaenidae: Catalog of species. *Tryonia* **12**: ii + 479 pp.

Richardson, C. L. 1986. Polygyracea: Catalog of species (parts 1, Polygyridae; 2, Corillidae; 3, Sagdidae). *Tryonia* **13**: i + 1–139, 1–40, 1–38.

Richardson, C. L. 1988. Streptaxacea: Catalog of species. Part 1. Streptaxidae. *Tryonia* **16**: i + 326 pp.

Richardson, C. L. 1989. Streptaxacea: Catalog of species. Part II. Ammonitellidae, Chlamydephoridae, Haplotrematidae, Rhytididae, Systrophiidae. *Tryonia* **18**: i + 154 pp.

Richardson, C. L. 1990. Partulidae: Catalog of species. *Tryonia* **19**: i + 96 pp.

Richardson, C. L. 1991. Urocoptidae: Catalog of species. *Tryonia* **22**: i + 245 pp.

Richardson, C. L. 1992. Cerionidae: Catalog of species. *Tryonia* **25**: 121 pp.

Richardson, C. L. 1993. Bulimulacea: Catalog of species. Amphibulimulidae, Anadromidae, Grangerellidae, Odontostomidae, Orthalicidae. *Tryonia* **27**: v + 164 pp.

Richardson, C. L. 1995. Bulimulidae: Catalog of species. *Tryonia* **28**: ii + 458 pp.

Rosenberg, G. 1992. *The Encyclopedia of Seashells*. Dorset Press, New York, New York.

Rosenberg, G. 1997. Biotic databases, the interface of taxonomic and collection databases. *ASC Newsletter* **25**: 13–14, 21.

Rosenberg, G. 2009. *Malacolog Version 4.1.1. A database of Western Atlantic marine Mollusca.* URL http://www.malacolog.org/.

Rosenberg, G., W. F. Ponder, P. U. Middelfart, T. M. Gosliner, P. Bouchet and P. J. Morris. 2002. *A biotic database of Indo-Pacific marine mollusks.* URL http://clade.ansp.org/obis/. Accessed 16 April 2014.

Saurin, E. 1958. Pyramidellidae de Pho-Hai (Sud Viêt-Nam). *Annales de le Faculté des Sciences (Saigon)* **1958**: 63–86, pl. 1–4.

Saurin, E. 1959. Pyramidellidae de Nhatrang (Vietnam). *Annales de la Faculté des Sciences (Saigon)* **1959**: 223–283, pls. 1–9.

Saurin, E. 1962. Pyramidellidae du Golfe de Thailande. *Annales de la Faculté des Sciences (Saigon)* **1961**: 231–266, pls. 1–5. [In French].

Schileyko, A. A. 1998–2007. Treatise on Recent terrestrial pulmonate molluscs. *Ruthenica Supplement* 2, 15 vols., 2210 pp.

Snyder, M. A. 2003. Catalogue of the marine gastropod family Fasciolariidae. *Special Publication of the Academy of Natural Sciences* **21**: iv + 431 pp.

Solem, A. 1990. How many Hawaiian land snail species are left? And what we can do for them. *Bishop Museum Occasional Papers* **30**: 27–40.

Sterba, G. H. W. 2004. *Olividae: A Collectors Guide (Mollusca, Neogastropoda)*. ConchBooks, Hackenheim, Germany.

Strong, E. E., O. Gargominy, W. F. Ponder, and P. Bouchet. 2008. Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia* **595**: 149–166.

Sykes, E. R. 1901. Conchology at the dawn and close of the nineteenth century. *Journal of Conchology* **10**: 35–42.

Tucker, J. K. 2004. Catalog of Recent and fossil turrids (Mollusca: Gastropoda). *Zootaxa* **682**: 1–1295.

Uetz, P. 2010. The original descriptions of reptiles. *Zootaxa* **2334**: 59–68.

Watters, G. T. 2006. *The Caribbean Land Snail Family Annulariidae: A Revision of the Higher Taxa and a Catalog of the Species*. Backhuys, Leiden, Netherlands.

Wells, S. M. 1995. Molluscs and the conservation of biodiversity. Pp. 21–26 *in* A. C. van Bruggen, A. C., S. M. Wells, and T. C. M. Kemperman. *Biodiversity and conservation of the Mollusca*. Backhuys, Oegstgeest-Leiden, Netherlands.

Wiktor, A. 1999. Agriolimacidae (Gastropoda: Pulmonata): A systematic monograph. *Annales Zoologici* **49**: 347–540.

Submitted: 20 April 2014; **accepted:** 30 May 2014;
final revisions received: 3 July 2014